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NOTES ON THE BEHAVIOR OF THE ANT-LION WITH EMPHASIS ON THE FEEDING ACTIVITIES AND LETISIMULATION.

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INTRODUCTION.

The ant-lion is one of the marvels of the insect world and is discussed in practically every text-book on entomology and in almost every popular book on insects. With the exception of results derived from attempts to analyze the behavior of these insects into tropisms (4), European papers may be epitomized as follows: (1) the pits are formed in sand that is protected from the weather; (2) the larva excavates this pit by moving backward in a constantly narrowing spiral and using its abdomen as a plowshare and its head for a shovel; (3) with one of its forelegs, the ant-lion scrapes the sand on to its head from the inner side of the spiral; (4) with its body entirely concealed, the larva lies in ambush, with its open jaws resting in the bottom of the finished pit; (5) by tossing up sand at random, the ant-lion forces insects that alight on the side of the pit to tumble to the bottom; (6) any small terrestrial invertebrate may become its prey; (7) there is no mouth opening, the food being imbibed through tubes formed by each mandible and another mouth-part.

In American scientific journals, I have been able to find only four articles treating of our ant-lion. The first and the longest of these is by Emerton (6). In the fall of 1870, he found a pit of *Myrmeleon immaculatus* De Geer, under the shade of a boulder, at Danvers, Mass. The larva was carried home and placed in a bowl of sand. Immediately it buried itself. After remaining beneath the surface for several days, it excavated a pit. No

mention is made of the larva using the foreleg to shovel sand on the flat head in the manner described by European and American popular writers. The larva was fed with flies. When given more than one at a time, it would kill all before eating any. It was kept over winter in a warm room. In May it spun its cocoon beneath the sand. In June the adult emerged, leaving half its pupa skin in the cocoon.

In August, 1871, Birge (2) found a colony of 600 ant-lions, under an overhanging cliff, in Albany County, N. Y. These pits were in a soil composed of fine disintegrated limestone commingled with pebbles and minute fragments of stone. Whenever an insect alighted upon the sides of the pit the ant-lion began to toss up the soil in all directions.

Moody (14) states that the ant-lion observed by him rests at the bottom of the pit with its jaws only showing, and that it throws up sand at escaping prey. It formed its cocoon June 4 and emerged July 8.

Moffat (13) writes: "Fine loose sand is evidently a necessity of their existence in any locality." He mentions the throwing up of sand when an ant steps on the side of the pit.

The Pit.

Most accounts give the erroneous impression that the pits of ant-lions are formed only in sand. Even in a scientific magazine, Moffat (13) writes, "Fine loose sand is evidently a necessity of their existence in any locality." A loose friable soil protected, more or less, from rain and shielded from chickens and similar insect feeders is all that is needed. It may be anything from the finest dust to coarse sand. In open sheds with dirt floors, under porches where the place is not too dark, beneath low railroad bridges that span sandy, dusty, or cindery ground, under ledges of rock, and beneath the shelter of logs that do not touch the ground at all points are good places to look for them. From time to time, during the past three years, I have had, in my insectary, more than 500 ant-lions. Many of these were obtained in Kansas by my friend, Mr. Phil Rau; the remainder were collected in and about St. Louis. The majority of these were found in the loamy clay (loess) that forms much of the top

soil of Missouri and Kansas; some were found in cinders in sheltered places along railroad tracks; some, in disintegrated mortar along the walls of buildings; some, in the rotton-wood dust of hollow logs; none of these was obtained from sand. In the wide jelly glasses of my insectary, where each larva was kept in solitary confinement, some were placed in loamy clay, some in sifted coal ashes, some in coal ashes that had been weathered for a year, some in fine sand and others in coarse. The larvæ seemed to flourish as well in one medium as in the other.

The ant-lion usually begins the construction of its pit by striking out a circle in the friable earth. Using its abdomen as a plowshare and its head as a shovel, the larva burrows backward, in a circular path, just beneath the surface of the soil, tossing upward and outward the dirt that falls upon its head. Almost all of the articles that I have read state that this initial circle marks the outer boundary of the finished pit. With the American ant-lion of the Middle West this is not always so. In most cases observed by me the finished pit is wider than the diameter of this circle. In the first place, the falling inward of the soil as the excavation progresses enlarges the diameter. Then, too, the ant-lion sometimes enlarges the partly or apparently entirely completed pit. After this first circle is completed, within this the ant constructs, in a similar manner, a deeper adjacent circle and so on until the center is reached. Then, with the major portion of its body hidden in the walls of the pit and using its head and mandibles as a shovel, it tosses out the material from the bottom of the pit, until the dirt no longer runs down the sides.

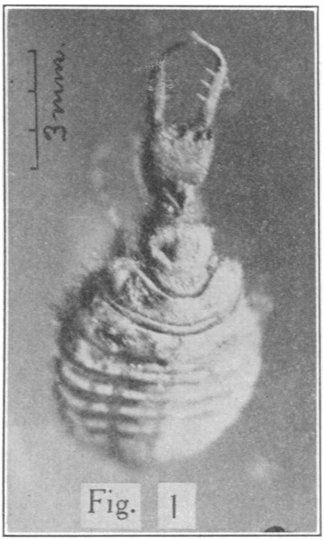
European writers state that the ant-lion shovels sand on to its head by means of one of its forefeet, and Kirby and Spence (8) insist that, in excavating its burrow, the ant-lion reverses the direction it is going at the completion of each circle, so as to alternately exercise each foreleg. In our American ant-lion this pair of forelegs functions, not as a scrape, but as a brace to the body when the ant-lion is shovelling dirt or turning. Patient watching with a magnifying glass has failed to detect the forefoot loading dirt upon the head; and certainly the ant-lion does not reverse the direction it is going every time it completes a

circle. The dirt gets upon the head by falling from above and from the sides, as the larva burrows backward through the soil. Some of this material comes from the outer edge as well as from the inner. While constructing its pit, the larva often pauses. After each rest it usually continues in the direction that it was going. On rare occasions, it does turn about and go in the opposite direction. This is usually when it has met some obstruction.

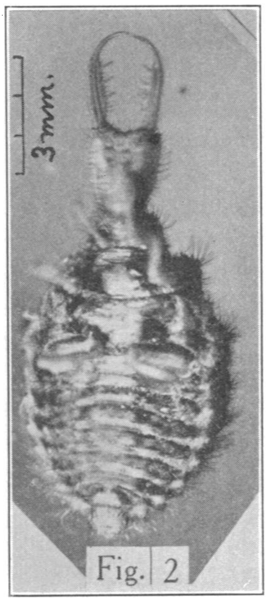
To test the matter more thoroughly, a sufficient portion of each of the forelegs of an ant-lion was amputated to render them much too short to be of value in shovelling soil on to the head. As soon as it was returned to its glass, the larva burrowed backward into the soil. For four days it remained beneath the surface. On that day it excavated a small pit. The next day the pit had been enlarged. On this day it was fed with ants (*Formica subsericea*). The ant-lion was then removed from the soil and examined under a simple microscope. The legs had not regenerated; each stump was covered with a ball of soil. This ant-lion had constructed its burrow without using its front feet as scrapers with which to load dirt on the head.

The force with which an ant-lion tosses the materials from its pit is astonishing. Often they are cast several inches beyond the rim. Sometimes the larva encounters particles which cannot be disposed of with a toss of the head. When these are not too heavy the insect has an unique method of disposing of them. The insect backs up the side of the pit with the obstacle poised on the posterior portion of its abdomen and deposits it beyond the edge of the pit. Although this behavior is described by Bingley (19), most writers do not mention it. Perhaps it sounds too much like a fairy tale; yet it is comparatively easy to induce an ant-lion to behave in this manner. I frequently induced it either by placing a small stone in the center of the ring of a pit that was being constructed; or, by depositing a similar object in the bottom of a completed pit. When the stone is placed in the center of the ring, as the ant burrows spirally inward, there is sure to come a time when the stone will fall into the furrow. When the ant-lion returns to that point it encounters the obstacle. Usually it burrows under the object and continues on part of

the way around the circle. Then, turning, it backs through the furrow thus made until it has inserted the tip of its abdomen under the impediment. It then backs slowly up the slope with the burden poised upon the tip of its abdomen. The edges of the abdominal somites and the stiff bristles thereon prevent the stone from slipping forward; while the dirt on each side prevents it from falling sidewise. Throughout this entire upward journey the whole body of the ant-lion is above the ground. It is an astonishing sight to see the insect backing, in almost a straight



Larval ant-lion. Dorsal view.



Larval ant-lion. Ventral view.

line, up the steep slope, with the burden poised on its back. When the burden has been disposed of, usually at the edge of the pit, the ant-lion turns about and returns to the bottom of the pit, usually in the furrow made by the upward struggle, and continues her digging. The furrows made before my eyes have always been straight or nearly so; but, one made in my absence was quite curved. When the object was placed in the bottom of a finished pit, sometimes the object was allowed to remain; but, in most cases, sooner or later, it would be removed, in the follow-

ing manner. When it had tossed up a few loads of dirt, the larva would back away from the obstacle in a straight or a curved line; then turning, it would back through the furrow thus made and proceed as described above. When the stone is too heavy for the insect to handle in the manner mentioned above, it either deepens the pit on one side of the obstacle, or buries the obstacle by mining under it, or else abandons the pit. In several important respects the behavior observed by me differs from that described by Bingley; (1) never once did I see the stone fall from the insect's back and roll to the bottom of the pit, (2) obstacles encountered in constructing the pit were usually removed at once, (3) such bodies were usually deposited just beyond the rim of the pit, (4) occasionally they were left on the side of the pit.

On rare occasions I have seen pits constructed in a different manner. Instead of beginning by striking out a circle, the ant-lion burrowed downward into the ground and began at once casting out the soil, thus making a pit of small diameter. Usually such pits were afterwards enlarged by burrowing into the walls and proceeding about as described above.

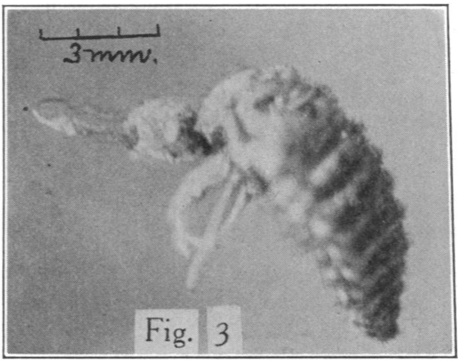
Thus my experience with the pit-building behavior of the ant-lion harmonizes with McCook's account (10); but is not in accord with that of Mrs. Comstock (5) who writes: "Wonderful stories are told about the way ant-lions dig their pits, marking out the outer margin in a circle and working inward. However, our common ant-lion of the East simply digs down into the sand and flips the sand out until it makes a pit."

The magnitude of the pit and the slope of the sides depend upon the size of the larva and the nature of the soil; the coarser the individual particles and the greater their specific gravity the more gentle the slope. In the loess about here the pits vary in diameter from less than half an inch to about two inches; the latter being the more abundant. Often the depth of the pit is almost as great as the diameter. Although a small ant-lion usually excavates a small pit, a small pit does not necessarily contain a small larva; for large larvæ sometimes construct small pits which they afterwards enlarge.

Occasionally one finds an isolated ant-lion pit; usually they occur in groups (Figs. 10, 11). In the same cluster the ant-lions

differ much in size, and this is true even in the early spring. Certain writers attribute these differences in size to the fact that some obtain more food than others. The following simple experiment lends support to this view. From a certain well-circumscribed area, containing about fifty ant-lion pits, a dozen larvæ were removed, on June 22, and placed in my insectary. A portion of these were well fed daily, the remainder were fed only occasionally. A few were lost by accidents. By August 8 all of the survivors of the well-fed lot had formed cocoons and a few imagoes had emerged. The poorly fed individuals were still larvæ. The majority of those left in the field were still larvæ.

Morphologically the ant-lion (Figs. 1–3) is well adapted to this pit-building behavior. The flat head, which, with the stout mandibles, forms an excellent shovel, is so articulated to the rest



Larval ant-lion. Lateral view.

of the body that it is possible to give it a powerful upward jerk. The abdomen is flat on the ventral and convex on the dorsal side, the whole tapering toward the tip in such a manner as to form an excellent burrowing instrument. From the sides of the body clusters of stiff bristles project outward and forward in such a manner that the body is prevented from slipping forward after it once has penetrated the earth. Then, too, the terminal claws on the legs (Fig. 12) make efficient anchors. The front of the dorsal portion of the prothorax is so rounded that dirt easily

falls forward and loads the shovel-like head. There is no functional anal opening; hence there is no danger of vigorous thrusts of the abdomen clogging the intestine with dirt.

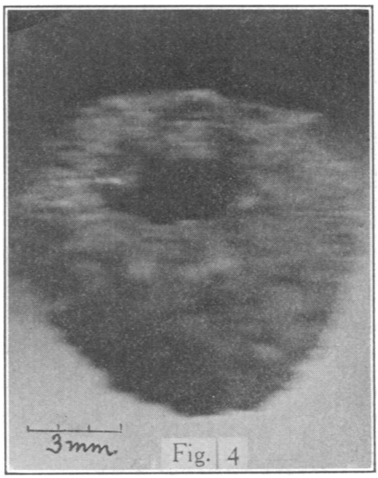
Feeding Behavior.

The finished pit is an inverted hollow cone, at the apex of which the wide-open mandibles of the larva, with their sharp teeth, await to grasp any unfortunate that happens to fall therein. What an efficient trap for small creeping invertebrates! The steep and unstable sides often cause the animals to fall to the bottom. If the intruder does not at once slide to the bottom, its struggles to escape tumble the soil upon the mandibles of the waiting ant-lion. Immediately the ant-lion begins to toss the soil upwards. The claim that the dirt is cast at the struggling creature is erroneous. Digging its mandibles edgewise into the bottom of the side of the pit, the ant-lion shovels out head-load after head-load of soil. It is not thrown at something; it is simply tossed upward and outward. Some of these random shots may take effect; and the constant undermining of the walls of the pit produces miniature landslides which, usually, drag the prey to the bottom of the trap.

Until something falls into the pit or alights on its treacherous sides, these mandibles of the larva usually rest horizontally in line with the body, which is hidden in the wall of the pit. Ordinarily the pits appear to be empty, for the mandibles are often covered with fine dirt. Even when the whole head is uncovered, its color harmonizes so perfectly with that of the soil as to render it invisible. As soon as its jaws close upon a creature the ant-lion backs deeper into the walls of the pit and, by interring its victim, subdues it. Thus the ant-lion is enabled to conquer creatures that are much larger and apparently stronger than it. Unless its first few struggles free it, the captive is doomed; for the ant-lion slowly but surely drags it deeper and deeper into the soil, while it feasts on its body juices. To assist in holding the prey while its body contents are being imbibed through the hollow mandibles, each mandible is provided, on its inner surface, with three stout teeth (Fig. 13*A*).

MacLachlan (11), in discussing the feeding of the European

ant-lion (*Myrmeleon formicarius*) says: "The house flies and other small insects were usually dragged partially or wholly under the sand, whilst blue-bottles and similar bulky creatures were feasted upon on the surface." In his account of the feeding of the common ant-lion of the east, McCook remarks: "The ants were held off at 'arm's-length,' so to speak, and were thrashed and jerked about until they were exhausted. Meanwhile efforts at defence were made futile by the captor, who held its victim out of reach of any vital part." Neither of these accounts tallies exactly with my experience, although MacLachlan's can be harmonized with it. I have watched ant-lions feed thousands of times and have fed them with a variety of invertebrates. In every case the larva has attempted to drag its captive beneath the ground. In no case was the insect held off at arm's length



Empty cocoon of ant-lion.

as described by McCook. Often, a few moments after its capture, all that would be visible of an ant were the tips of its waving antennæ, or the extremity of its wriggling abdomen, or both. Naturally the captive struggled and squirmed; but there was no attempt on the part of the ant-lion to hold its prey at arm's length above the ground, while it thrashed it and jerked it. If the first closing of the mandibles does not capture the creature that

happens to fall into the pit, remaining at its post, the ant-lion elevates its head and makes repeated snaps at the creature as long as it remains near. It may be that the ocelli located at the base of the mandibles, on the dorsal side of the head, aid in this.

The name ant-lion is a misnomer; for it creates the impression that this insect feeds exclusively, or almost exclusively, upon ants. Such is not the case. Any small creeping invertebrate—be it insect, crustacean, or arachnid—is acceptable. Several of the most flourishing colonies of ant-lions found near St. Louis are located in the dirt floor of a dilapidated stone-crusher of an abandoned quarry. The diet of the inmates of those pits is composed largely of sow-bugs (*Porcellio*). Emerton (6) and MacLachlan (11) fed their ant-lions on living flies that had been disabled; Berce (1) reared his on living flies, wood-lice and earwigs. I supplied mine with

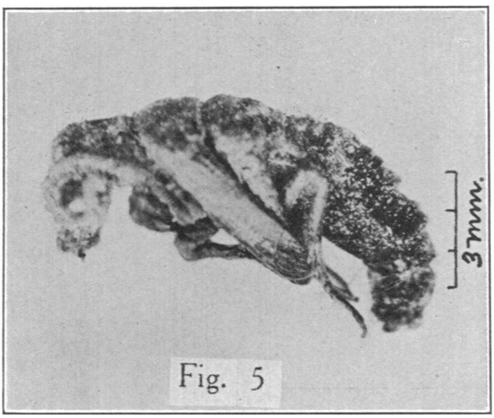


FIG. 5. Chrysalis of ant-lion that died on way to surface.

living specimens of the following invertebrates; caterpillars (even hairy ones), wood-lice, small roaches, small moths (held by the wings until the ant-lion had secured a hold), spiders, nymphal squash bugs, ants, small beetle larvæ, soft-bodied beetles, and bed-bugs. All of these were accepted and, after the juice had been sucked from each body, the dried remains were cast out of the pit.

The ant-lion has no mouth opening in the true sense of the word. The strong curved mandibles are perforated at the tip,

and along the ventral surface of each there runs a prominent tube through which the juices of the victim are sucked. This tube is composed of two parts. Along the whole of the ventral surface of each mandible [Fig. 13*A*] there is a deep groove with incurved edges. Another mouth part [Fig. 13*B*], probably the maxilla, fits so tightly into this groove of the mandible that, even when viewed with a 2/3-inch objective, the two seem to form a single structure. With that power, on the underside of each mandible one sees two ridges. These mark the junctions of the two pieces; but, unless you had previously dissected a mandible, you would not suspect that there were two pieces and that they were not rigidly united. Turn the insect on its ventral surface,

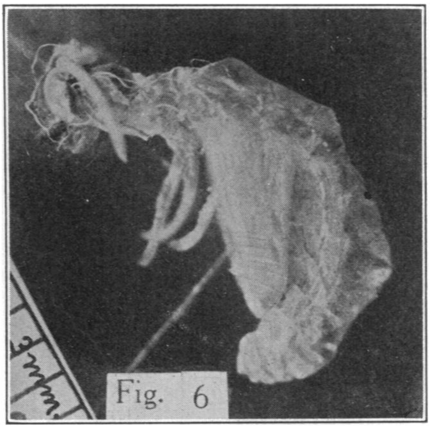


FIG. 6. Shed chrysalis skin of ant-lion.

carefully disarticulate the mandible, and, with a pair of dissecting needles, gently push it forward. Thus the other mouth part will be gradually drawn out of the mandible and left attached to the ventral part of the front of the head.

The ant-lion preys upon living invertebrates. How does it distinguish the living from the not-living? There may be several factors which help it solve this problem. The following experiments show that one attribute by means of which the ant-lion differentiates between desirable and undesirable prey is the exhibition of restlessness:

Experiment 1.—I fastened a bit of straw to the end of a silk thread.

Twirling the other end of the thread between my thumb and fore-finger, I gently lowered it to the bottom of the pit. Three times in succession the ant-lion caught hold of the straw with its mandibles. Each time I jerked the string and thus removed the straw from its grasp.

Experiment 2.—I fastened a dead chinch bug to one end of a silk thread. Twirling the other end of the thread between my thumb and fore-finger, I gently lowered the bug to the bottom of the pit. Immediately the ant-lion seized it with its mandibles and held on until, by pulling on the thread, I had drawn the insect partly out of the pit. This experiment was tried with five different individuals. Four responded in the manner just described; the fifth made no response.

Experiment 3.—I fastened a piece of cotton to one end of a silk thread. Twirling the other end between my thumb and fore-finger, I gently lowered it to the bottom of the pit. The ant-lion gripped the bit of cotton with its mandibles and held on until I, by pulling on the thread, had dragged the larva partly out of the pit. This experiment was tried with five different individuals. The result was always the same.

MacLachlan (11), in 1864, placed between two and three dozen ant-lions in a small box of sand and carried them from Fontainbleu, France, to London. When he arrived, about half of the larvæ had been killed and the juices of their bodies extracted by the others. In shipping ant-lions to me from Kansas, Mr. Rau placed a hundred or more in the same small box of dirt. In sorting over the material to place each one in an individual retainer, I always found several dead specimens that looked as though the juices of their bodies had been extracted. Are these deaths caused by cannibalism? To test the matter, an ant-lion was dropped into the pit of another individual. This experiment was repeated over and over again throughout a summer devoted largely to the field study of this creature. In the majority of cases the intruder escaped either by burrowing into the wall of the pit or else by backing out of it. In several instances, however, it became the prey of the rightful owner of the pit. Evidently, when opportunity permits, this creature is a cannibal.

Locomotion.

The forms of locomotion used in excavating pits and in removing obstacles therefrom have been described in the section on "The Pit" and will not be repeated here.

When placed on loose dry soil, the ant-lion may letisimulate. As soon as it begins to move, it burrows backward into the ground. If an ant-lion is placed in an open rectangular pasteboard box, it backs along, sometimes in a straight line and sometimes in a curved line, until it comes in contact with one of the sides. It then backs along that side until it comes to a corner, turning the corner it continues along to the next corner. It may continue thus for a long time, or it may vary it by creeping backwards up

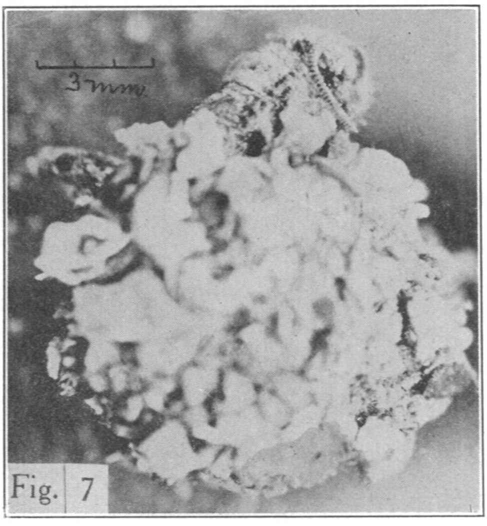


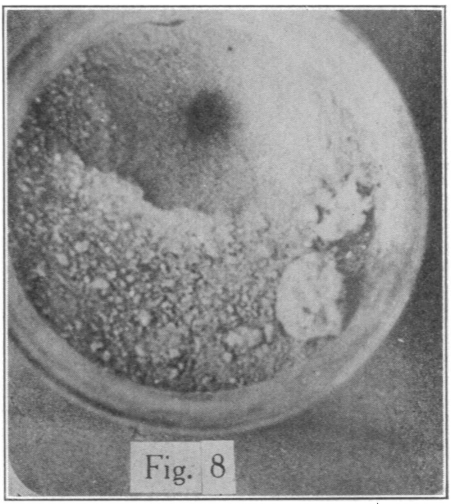
Fig. 7. Cocoon of ant-lion, with chrysalis partly emerged. This cocoon is from a form that was raised in shifted coal ashes.

one of the angles until it reaches the top of the box and then pass downward to the ground. After it has once reached the side of the box, no matter how long it remains within the box, it almost never moves out into the open. These two simple experiments indicate that this insect is positively thigmotactic. With this statement must be coupled the reservation that, at times, the creature moves about with all of the upper portion of the body

exposed. This is the case when it is removing an obstacle from its pit.

Since this larva burrows downward into the earth, it may be considered positively geotactic; but, it must be remembered that it does not always pass downward. When disturbed in its pit, it usually backs upward, just beneath the surface, until the rim is reached; sometimes, it continues onward, in a horizontal direction, beneath the surface. MacLachlan (11) observed that, at night, they frequently make perigrinations over the surface of the ground. Then, too, they sometimes ascend vertical surfaces.

When placed on a horizontal surface [I used sheets of brass,

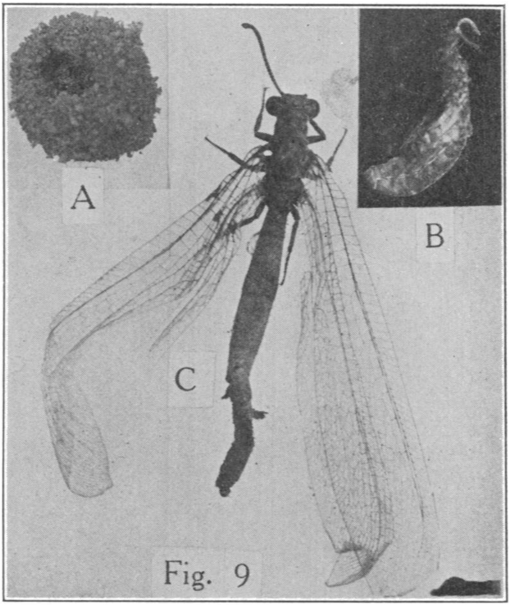


Ant-lion pit in one of my tumblers.

glass, wood, and cardboard], the larva backs away from the light. If placed with the tip of its abdomen toward the source of light, usually, it will move a short distance toward the light then turn, to either the right or the left, and back away in a straight line. This, coupled with the fact that, when placed on its back, the ant-lion invariably rights itself by turning away from the source of light, induces the conclusion that this creature is negatively phototactic; but, it must be remembered that in

constructing its burrow the larva crosses the light at every possible angle, and that, at times, it moves toward the light.

This insect invariably moves backward; never under any conditions does it move forward; yet it is capable of performing all the ambulatory feats possible to an insect that progresses in the orthodox way. It can move in a straight line, it can describe simple or s-shaped curves to either the right or the left, and it can ascend or descend rough surfaces inclined at any angle from zero to ninety degrees. By means of what structures does it perform these movements? Are they produced entirely by flexing the abdomen and trusting to the body bristles to prevent



Photograph showing the comparative size of cocoon, chrysalis and imago. They belong to the same ant-lion and are photographed to the same scale. *A*, cocoon; *B*, chrysalis skin; *C*, imago.

forward movements? Do the legs take any part in the movements? Do the mandibles assist? To answer these questions the following experiments were devised.

Experiment 1.—An ant-lion was placed on a glass plate arranged horizontally. By means of a hand magnifying glass every movement

was watched. It moved backward in jerks. The hind legs, which were doubled back under its abdomen, made jerky pulls. The middle pair of legs was directed outwards in almost a straight line. The anterior pair of legs was stretched forward. The tips of both the first and second pair of legs touched the glass. The mandibles took no part in the movement.

Experiment 2.—The ant-lion was placed on the glass plate and held, in a horizontal position, above my head; so that I could look up at it with a magnifying glass. The results were the same as in experiment 1; but it was easier to observe that the tips of all the legs touched the glass. The third pair of legs was the only pair making vigorous movements.

Experiment 3.—I tilted the glass plate so that the posterior portion of the ant-lion was uphill. When the angle became steep the ant-lion fell.

Experiment 4.—Repeated number 1, substituting a pasteboard rectangle for the glass plate. The result was the same as in experiment 1; but the insect moved faster.

Experiment 5.—I tilted the paste-board rectangle so as to have the posterior portion of the insect up-hill. Even when it had reached an angle of 90 degrees, the insect retained its hold. It moved upward, sidewise and downward.

Experiment 6.—While the cardboard rectangle was inclined at a steep angle and the ant-lion was resting head downward, with a dissecting needle, I raised the tip of the abdomen from the support. The ant-lion retained its hold.

These experiments show conclusively that the mandibles do not assist in locomotion; at the same time, they indicate that the hind pair of legs play an important rôle. Yet, so far as these experiments go, the hind legs might be mere grappling hooks to prevent the creature from slipping forward and the real locomotion be due entirely to the flexing and stretching of the abdomen, all forward motion being prevented by the stiff bristles on the sides of the body and the grip of the legs.

Experiment 7.—A layer of dirt equal to the height of the greatest height of the ant-lion was spread on a glass plate. The ant-lion was placed on this pile of dirt. The larva began to burrow backward into the dirt; but made practically no progress. By the

behavior of the body I could see that it was making vigorous movements with its third pair of legs; but it made practically no progress.

Experiment 8.—A layer of dirt equal in elevation to the greatest height of the ant-lion was placed on a pasteboard rectangle. An ant-lion was placed on this pile of dirt. Immediately it began to burrow backward and continued to progress at a rapid rate.

(In all of the experiments from 1–8 the same individual was used. The series was repeated many times with different in-

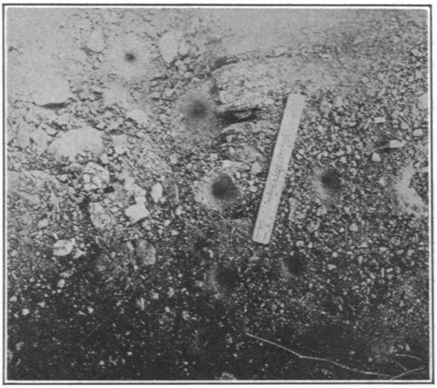


FIG. 10. A cluster of ant-lion pits (average cluster).

dividuals; but, in each case, the same individual was put through the eight experiments.)

In experiments 7 and 8 the presence of the dirt makes it necessary for more work to be performed in making progress backward. Since the height of the pile is the same in each case, the amount of work required is the same. Since the bristles are more numerous on the sides of the body than on the ventral surface, the presence of the dirt should give an added opportunity for them to function in preventing forward slipping of the body; hence, if the progress is due simply to a flexing and stretching of the body the ant-lion should be able to move just as fast, if not faster, on a glass plate with a layer of soil as on the naked glass. If, however, the hind legs play an important rôle in dragging the body backward, then the larva on the dirt-covered pasteboard should have a great advantage over the one on the dirt-covered glass plate. These

experiments prove, I think, that the hind legs assist in dragging the body backward. A microscopic examination of the legs reveals two terminal claws which function in this work (Fig. 12).

Emergence of the Imago.

This section does not pretend to be a life history of the ant-lion. That the author hopes to make the subject of a future paper. This is simply an attempt to state some interesting facts about the last stages of the metamorphosis.

At the close of its larval period, the ant-lion constructs a subterranean spherical cocoon of silk and soil. In my insectary, most of the cocoons have been formed quite near the surface; sometimes projecting slightly above the soil. In one case, however, I found a cocoon on the bottom of the jelly glass,

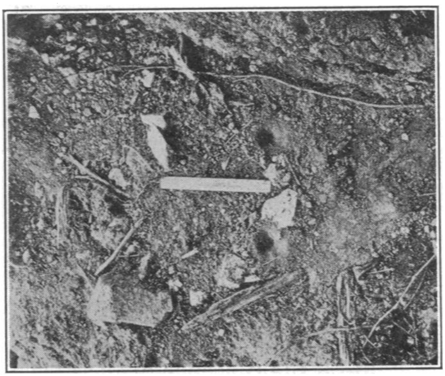


Fig. 11. A cluster of ant-lion pits (small cluster).

fully two inches below the surface. In my insectary, the cocoons have been formed in July and in August and the imagoes have emerged in from 9–20 days thereafter; but I do not consider that I have sufficient data to warrant the statement that they are always formed at those times.

Inside of this cocoon the insect sheds its last larval skin and becomes a chrysalis. At the end of a certain period of time the anterior portion of the thorax protrudes from the cocoon (Fig. 7).

All of the accounts that I have read state that the chrysalis comes about half way out of the cocoon and from its dorsal

surface the imago emerges. In my limited experience I have noticed three methods of emergence. In one case the chrysalis protruded about half way out of the cocoon and the imago emerged from its back. In another case the chrysalis had left the cocoon entirely and protruded about half way out of the soil. In the third case both the head end and the tail end of the chrysalis remained within the cocoon and from its back the imago emerged. I am inclined to think the third case abnormal, caused by the head of the chrysalis becoming entangled in some strands of the cocoon. Fig. 6 is a photograph of the cast skin of that chrysalis, made just after I had removed it from its cocoon. It seems to me that the other two cases may be explained as follows: when

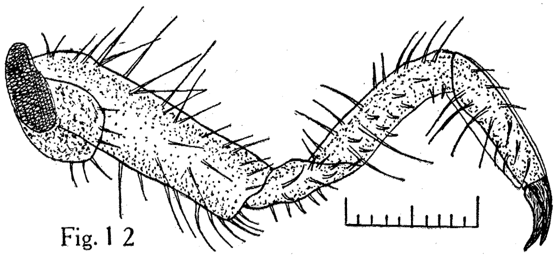


Fig. 1 2

FIG. 12. One of the third pair of legs of an ant-lion larva.

the cocoon is near enough to the surface for the chrysalis to expose the upper portion of its body without coming entirely out of the cocoon it does so; when the cocoon is a little deeper then the chrysalis leaves the cocoon entirely and continues upward until the anterior portion of its body is above the surface.

When the cocoon is too far beneath the surface, the chrysalis dies on its upward journey. Fig. 5 is the photograph of such a chrysalis. It was found dead about half an inch below the surface. Attached to the bottom of the jelly-glass—about an inch below—the empty cocoon was found.

Soon after emerging the imago undergoes an enormous increase in size. It soon becomes more than twice as large as the chrysalis from which it came, and this without partaking of food. Fig. 9 illustrates this. The jelly glass containing the cocoon had been tightly closed to prevent the possible escape of the imago when it emerged. It emerged at an unexpected time and when discovered it was dead. It had lost one antenna and its body was

slightly damaged. Under the conditions it could not possibly have obtained food. Half exposed above the soil was the shed chrysalis skin, and a short distance below the surface the empty cocoon (Fig. 4) was found.

Miscellaneous Activities.

Experiment 1.—A ring of water eight inches in diameter was made on a glass plate and an ant-lion placed in the center of the dry space that the ring surrounded. The ring was one half of an inch in width. When the ant-lion reached the ring of water, it would usually turn and move away from it. Often, in turning, its mandibles would get into the water. In that case the mandibles would

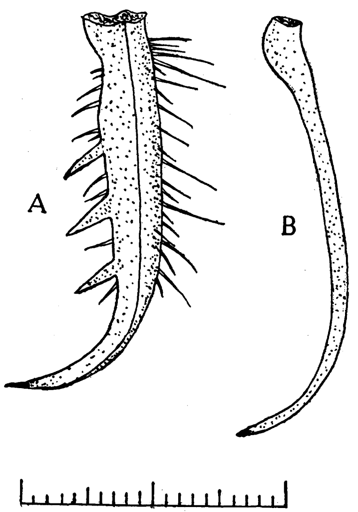


FIG. 13. The parts that form the sucking tube of the ant-lion larva. *A*, mandible. *B*, the part that fits into the groove of the mandible.

leave a broad water band wherever the creature went. After its mandibles had become wet, on its next approach to the water, it was apt to get some other part of its body wet. After that it was apt to move, away from the light, on through the water.

Experiment 2.—To see if there was anything about dirt as such that would direct an ant-lion to it, a pile of dirt three inches in diameter was placed in the center of a glass plate that was twelve inches

square. The ant-lion was placed at various places near the periphery of the plate. Unless the ant-lion was placed in such a position that in going directly away from the light it would encounter the dirt, never once did an ant-lion discover it. Sometimes the larva passed within less than a centimeter of the dirt without being attracted by it.

LETISIMULATION.

Letisimulation (from *letum*, death, and *simulare*, to feign) is a term coined by Weir[1] in 1899, to designate the death-like attitude assumed by individuals of many different groups of the animal kingdom, when roughly handled. While citing examples from among the worms, insects, reptiles, birds, and certain mammals, he leaves the impression that the most remarkable examples of death-feigning are to be found among the reptiles and certain mammals. Since that time much careful attention has been given to the letisimulation of insects. Barret (22) has studied it in the mole-cricket; Gee and Lathrop (26), and Johnson and Girault (32), in the plum curculio; Girault (27), in trox; Holmes (30), in the water scorpions; Newell (34) and Weiss (40), in the rice weevil; Riley (36), in dragon-fly nymphs; the Severins (37), in the giant water bugs, and Wodsedalek (41, 42), in May-fly nymphs and in a dermestid larva. In the light of the remarkable traits revealed by these investigators, were he writing his article today, Weir, no doubt, would agree with Homes that "it is among the insects that the death-feigning instinct reaches its highest development, occurring in a greater or less extent, in most of the orders. It is especially common in beetles and not unusual among bugs, but it is quite rare in the highest orders such as the Diptera, or flies, and the Hymenoptera, or ants, bees and their allies. It occurs in a few cases among the butterflies and moths, both in the imago as well as the larval state. The instinct is exhibited in different species in all stages of development from a momentary feint to the condition of intense vigor lasting for over an hour. Some insects may be severely mutilated, or, according to De Geer, even roasted over a fire before they cease feigning."

Although the activities of ant-lions have interested many

[1] Weir, "Dawn of Reason," pp. 202–214.

naturalists, very little attention has been paid to their death-feigning behavior. Emerton (6) asserts that rough handling caused his specimens to remain inactive for a time, and MacLachlan (11) states that the form observed by him letisimulates. Each of these students dismissed the matter with a single sentence.

The results recorded in this article are based on a careful laboratory study of 100 individuals selected at random; supplemented by observations made in the field. About 60 per cent. of these came from Kansas; the remainder from the vicinity of St. Louis, Mo. Some were quite small and others were almost large enough to form their cocoons. They were isolated in numbered jelly-glasses, partly filled with loamy loess, and were kept in an out-of-doors insectary, the north wall of which was constructed of wire netting. The other walls were opaque.

Any stimulus which produces a shock will usually cause an ant-lion to letisimulate. Rough handling, roughly turning it upon its back, dropping it from a slight elevation, all have a similar effect. I usually induced the feint by roughly turning the larva upon its back, or by dropping it from a slight elevation. Occasionally I found an individual that I could not induce to letisimulate; but this was a very rare occurrence.

Several investigators have thought it important to determine if the poses of letisimulating individuals are death attitudes. Based on a consideration of seventeen species of invertebrates, Holmes (31) concludes that the poses assumed were usually quite different from death attitudes; although there were some species in which they were always identical. I find that the ant-lion has not one, but several death attitudes; likewise it possesses a number of death-feigning postures, some of which resemble a death pose and some of which do not. The insect suddenly becomes rigidly immobile in whatever attitude it may be when it receives the shock. Absolute immobility is the character that is common to all cases; when the feint follows a long period of fasting, this inactivity often simulates death. The rigidity, however, is not so great as that described for certain insects. In some species of insects the rigidity of the parts during a death feint is so great that the insect may be picked up by a tarsus and

held out at right-angles without the leg bending in the least. That is not the case with the ant-lion. When an attempt is made to lift it, in that manner, by a tarsus, the leg bends and the insect awakes from its feint.

When an ant-lion is recovering from a feint, usually, although not always, there is a preliminary waving of the antennæ and a twitching of the legs and, sometimes, a movement of the head. Then the larva suddenly turns over. Throughout the whole series of experiments, a careful record was kept as to whether the insect turned towards the right or towards the left; towards the light or away from it. It was found that whether the insect turned toward the right or toward the left depended upon the location of the strongest light; for the ant-lion invariably turns away from the light.

Pinching the legs of a letisimulating individual almost always caused it to come out of its feint. Blowing upon a death-feigning larva would sometimes bring no response; at others it would induce a twitching of the legs; at yet others it would cause a complete recovery. Since the pinching of a leg, and even attempts to lift the letisimulating ant-lion by a leg, usually terminates the feint, I was surprised at the results produced by the following mutilations.

Experiment 1.—With a pair of small, but sharp, dissecting scissors, I cut off the tip of a fore-leg of a letisimulating ant-lion. The insect did not respond.

Experiment 2.—With a pair of small, but sharp, dissecting scissors, I clipped off the tip of a mandible of a letisimulating ant-lion. The insect did not respond.

Experiment 3.—With a pair of small, but sharp, dissecting scissors, in rapid succession, I cut off the tips of both fore-legs and of a mandible of a letisimulating ant-lion. The insect did not respond.

Experiment 4.—With a pair of small, but sharp, scissors I severed the head from the body of a letisimulating ant-lion. The insect did not respond, nor did it recover from the operation.

Experiment 5.—A pair of small dissecting scissors, identical with those with which the above experiments were performed, was heated red hot, in a Bunsen flame, and allowed to cool. This softened the

steel and made the edges quite dull. With these scissors an attempt was made to remove the tip of a leg of a letisimulating ant-lion. The scissors were too dull to cut through the chitin; instead of being severed, the leg became wedged in between the blades. The feint was terminated immediately.

With the exception of experiment number four, these amputations were performed several times. On one occasion, a larva recovered the moment I cut a leg; on another day, the same thing happened when I severed a mandible. With these two exceptions, the results were always as stated above. How shall we harmonize the fact that the pinching of a leg or, sometimes, the blowing of the breath on the larva terminates the feint, while the severing of a leg, or a mandible, or both invokes no response? Shall we decide that such a pinch produces a greater physiological shock than a sudden cut with a pair of sharp scissors? Is it possible that a breath of air produces a greater shock than an amputation with sharp instruments?

Relative Duration of Successive Death Feints.—In his study of the beetle *Scarites gigas* Fabre (24) found that the duration of the first five successive feints gradually increased from the first to the last. The Severins (37), in their study of the giant water bugs *Belostoma* and *Nepa*, and Gee and Lathrop (26), in their study of the plum curculio (*Conotrachelus nemuphar*), find great irregularity in the lengths of the successive feints.

To test the matter, an ant-lion was removed from its pit, placed on a board, and made to letisimulate by roughly turning it on its back. As soon as it recovered from one feint, it was roughly turned on its back and induced to letisimulate again. This was repeated until it had had an opportunity to letisimulate twenty times. By means of a stop-watch, the duration of each feint was obtained. One hundred individuals were thus experimented with and the results recorded in a table. Criticially examined, the table revealed a number of interesting things. (1) There are marked individual variations. (2) In twenty opportunities the individual usually letisimulates less than twenty times. (3) The total time consumed in twenty opportunities to letisimulate varied from one minute to two hours and twenty-three minutes. The average for the 100 individuals was nineteen

and six-tenth minutes. (4) This death-feigning cannot be indefinitely prolonged. (5) The duration of the feints near the end of a long series of trials is always shorter than that of the earlier ones. (6) A curve representing the relative lengths of a series of letisimulations always contains two or more crests. (7) The longest feints usually occur somewhere near the beginning of the series. Of the 100 cases recorded, 33 letisimulated longest on the first trial, 11 on the second, 15 on the third, 2 on the fourth, 5 on the fifth, 7 on the sixth, 3 on the seventh, 5 on the eighth, 6 on the ninth, 5 on the tenth, 1 on the eleventh, 4 on the twelfth, 2 on the thirteenth, and 1 on the sixteenth. We have here, in a pronounced manner, the irregularity noticed by the Severins and Gee and Lathrop in the forms studied by them.

Effects of Temperature upon the Duration of Letisimulations.—To test this matter the 100 individuals mentioned were grouped according to the temperatures at which the experiments had been performed, and the results recorded in six tables. From the averages of those tables the following table was compiled.

TABLE SHOWING THE AVERAGES OF THE EFFECT OF TEMPERATURE ON THE LETISIMULATIONS.

Temperature in F. Degrees.	Number of Individuals Used.	Number of Letisimulations in Twenty Trials.	Maximum Time in Min. of a Single Letisimulation.	Number of the Trial on which Max. Let. was Made.	Total Time Consumed in Letisimulations.
60–65	7	15	3.35	4	14.19
65–70	12	16	6.86	2	26.11
70–75	17	17	7.25	5	35.11
75–80	23	13	3.97	5	13.06
80–90	17	12	5.91	6	13.30
85–90	21	9	3.83	6	12.15

If we were to rely upon these averages, we would conclude that up to 75° F. both the length of the maximum feint and the total duration of twenty feints vary directly with the temperature; and that beyond that point there is no definite relation between temperature and the feints. This conclusion, however, is not supported by a critical study of the individual records from which the averages were compiled. To test the matter further, four individuals were selected and each put through five series of twenty letisimulations, each series being conducted at a different temperature. The results were recorded in four tables. There

was no obvious relation between temperature and the duration of the feints.

Effects of the Strength of Stimulus upon Letisimulation.—To get the stimulus as nearly uniform as possible, the ant-lion was gently shoved from a glass ledge and caused to fall three inches. To secure a strong stimulus the ant-lion was permitted to fall upon a glass plate; to secure a weak one it was allowed to drop on a layer of cotton batting. The results of experimenting with 100 ant-lions was tabulated. In 36 cases the first letisimulation following a strong stimulus was the longer and in 58 cases the first feint following a weak stimulus was the longer. In six cases the duration of the feint was the same for each stimulus. The average of 100 individuals gave the duration of the first letisimulation following a weak stimulus as of longer duration than the first following a strong stimulus. These data do not seem to warrant a conclusion.

Effects of Hunger upon Letisimulation.—Certain selected individuals were well fed and others were forced to fast for a long time before they were used for experiments identical with those mentioned above. The results were carefully tabulated. No relation could be detected between hunger and the length of the letisimulation.

Apparently the reason for the longest letisimulation being located sometimes at one place and sometimes at another in the series is due to some internal (physiological) factor not revealed by these experiments.

Weir[1] considers the letisimulation of animals "one of the greatest evidences of intellectual action, on their part." Hamilton (29), Webster (39) and a few others feel that the creatures consciously fear death and take this means to avoid it. Dr. Lindsley, in "Mind in Animals," thinks "this must require great command in those that practice it." However, the majority of modern students of the subject look upon it as merely a remarkable instinct.

No one who is acquainted with how slowly the ant-lion recovers from injuries could, for a moment, consider anything intellectual, which induces it to passively submit to portions of its legs and of

[1] Weir, "Dawn of Reason," 1889, p. 202.

its mandibles being amputated. The tonic contraction of the muscles and the diminished reflex irritability suggest hypnotic phenomena and lead one to agree with Holmes (31) that "the instinct of feigning death is doubtless connected with much of what has been called hypnotism in the lower animals." It is well known that most animals pause momentarily when confronted with an unexpected or violent stimulus. To me the letisimulation of the ant-lion appears to be such a pause prolonged and exaggerated. The more I ponder over the results of my experiments upon the death-feigning of the ant-lion, the more I feel inclined to exclaim with James: "It really is no feigning of death at all and requires no self-command. It is simply terror paralysis which has been so useful as to become hereditary."

Conclusions.

1. The pits of the ant-lion are not confined to sand; they may be found in any kind of dry friable soil, that is protected from the rain and from insect-eating creatures. They are usually in clusters; but, occasionally, a solitary pit is found. On yet rarer occasions, pits may be found that are not under a shelter.

2. The ant-lion of the Middle West has two methods of excavating its pits. Usually it furrows backward, excavating a series of concentric, adjacent circles, each deeper than the last, and shovelling out the soil with its head. The front of the body is so curved as to make it easy for the dirt to fall forward on the head. In the second method, the larva simply burrows downward into the ground and tosses out the soil with its head until the sides of the pit become approximately stable. Pits formed by the second method are usually subsequently enlarged.

3. The ant-lion removes a medium sized obstacle from its pit by inserting the tip of its abdomen under it and, with the burden poised on its abdomen, backing slowly up the slope.

4. After its trap has been completed, the ant-lion rests quietly, in practically a horizontal position, with its body beneath the soil and its open mandibles in the bottom of the pit.

5. Any invertebrate, be it insect, arachnid, or crustacean, that happens to fall into the trap is acceptable food. Some escape, but the larva attempts to capture all. When captured, the

victim is dragged partly or wholly beneath the soil, and the juices imbibed through the hollow mandibles. Later the dried carcass is tossed away.

6. The ant-lion may be considered positively geotactic, positively thigmotactic and negatively phototactic; with the reservation that all of its movements cannot be explained as tropisms in the Loebian sense.

7. It is impossible for the ant-lion to move forward; but, in its backward movements, it can move in straight lines or curves, and can scale vertical surfaces that are not too smooth. The hind legs assist in producing this backward movement, and the other legs brace the body.

8. Sometimes it avoids water and at others it backs into it.

9. If the spherical cocoon of this insect is near the surface of the ground, the chrysalis comes only part of the way out and the imago emerges from its back. If the cocoon is at a slightly greater depth, the chrysalis comes entirely out of the cocoon and part of the way out of the ground. If the cocoon is at a greater depth, the chrysalis emerges entirely from the cocoon and perishes on the way to the surface of the ground.

10. Rough handling or dropping from a slight elevation will usually cause an ant-lion to letisimulate. The length of a feint and the position of the longest feint in a series of successive feints varies in different individuals and in the same individual at different times.

11. There is no obvious relation between the temperature, the strength of the stimulus, or fasting and the duration of a letisimulation.

12. If the relative durations of the successive feints of a long series of letisimulations are plotted, the curve will have two or more crests.

13. In the ant-lion all letisimulation poses are not death attitudes. The ant-lion has no characteristic death-feigning posture. It is to be grouped with those insects in which the letisumation pose varies with the attitude of the individual at the time when the stimulating shock is received.

14. Although pinching a leg and, sometimes, even blowing on the body, will usually cause a letisimulating ant-lion to come out

of its feint, in the majority of the cases, it will submit to the clipping off of the tips of its legs and of its mandibles without responding in any visible manner.

15. In the ant-lion letisimulation seems to be but an exaggerated prolongation of the pause made by most animals when they are startled. The total behavior of a death-feigning ant-lion supports Holmes's contention that "the instinct of feigning death is connected with much of what is called hypnotism in the lower animals"; and endorses James, when he says: "It is really no feigning of death at all and requires no self-command. It is simply terror paralysis which has become so useful as to become hereditary."

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